EFFECT OF BLACKENED EPAULETS ON THE TERRITORIAL BEHAVIOR AND BREEDING SUCCESS OF MALE REDWINGED BLACKBIRDS, *AGELAIUS PHOENICEUS*[1]

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MORRIS, LYNN. The effect of blackened epaulets on the territorial behavior and breeding success of male redwinged blackbirds, *Agelaius phoeniceus*. Ohio J. Sci. 75(4): 168, 1975.

The epaulets or red shoulder patches of the male redwinged blackbird (*Agelaius phoeniceus*) were blackened during both the pre-breeding and post-breeding periods of the breeding cycle, 15 March to 1 June 1973. Male territorial defense was weakened in males with blackened epaulets as indicated by a higher than average trespass rate when compared with control birds. Males with blackened epaulets were able to mate and bring off a successful brood but experienced some difficulty, initially, in doing so as indicated by a delay in the courtship sequence. Adult males not previously seen to defend neighboring territories are selective of the area they will occupy. In marsh segments of low productivity studied during the pre-breeding period, new adult males were not seen to displace blackened epaulet resident males. During the post-breeding period, however, in marsh segments high in productivity, new adult male redwings were seen to occupy and defend a resident male's territory subsequent to his epaulet blackening and release. The new males may be able to mate in late May or June. They also may gain easier access to the productive territory for the following breeding season.

The male redwinged blackbird, *Agelaius phoeniceus*, spreads his wings displaying his bright red epaulets or shoulder patches in an aggresive response to trespassing males. The red epaulets, which provide distinct contrast in the plumage of the bird, function in the song spread display as a signal to other males that the terrtiory is occupied (Nero, 1956a). Peek (1971) blackened the epaulets of the male redwing blackbirds in different marsh-nesting populations during both the pre-breeding and post-breeding periods, and found that males with blackened epaulets were forced off their territories by adult males not previously seen to occupy neighboring territory. This occurred only during the pre-breeding period when territorial establishment was most intense. The pre-breeding period includes male territorial establishment, the arrival of the females one to three weeks later, and the beginning of establishment of pair bonds. Smith (1972) using similar techniques found that this new male population would occupy territories in the post-breeding period in the same proportion as the pre-breeding period. The post-breeding period is subsequent to mating and includes nest construction, incubation, and the beginning of the nestling stage. Because of differences in these findings, the effect of blackening the males' epaulets at different stages in the breeding cycle was reexamined.

METHODS AND MATERIALS

The study area was located on the North-central Branch Farm on the Ohio Agricultural Research and Development Center in western Erie County, Ohio. This farm has several marsh segments, three of which were used in this study. The marsh segments were separated by grassy dikes measuring only a few feet in diameter.

Observations and experimentation were carried out during the breeding season, 5 March to 1 June 1973. Two marsh segments were used for the study of the pre-breeding period, 15 March to 30 April. Since both segments were studied as a unit they were designated as Segment F. Segment F included 8.4 acres with a water level from only a fraction of an inch to several inches in depth. Marsh Segment C was used for the study of the post-breeding period, 30 April to 1 June. It covered an area of 10 acres with water levels varying from 1 ft to 2 ft. in depth. In all three segments, cattail-

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Typha latifolia, was the predominant form of vegetation. In addition, there was old field type vegetation such as dogwood (*Cornus* sp.), cottonwood (*Populus deltoides*), willow (*Salix* sp.), soft stem bulrush (*Scirpus validus*), and various sedges. A greater abundance of this old field type vegetation was found in Segment F than in Segment C.

Marsh Segment F was divided into squares 50 ft. on a side, and marked with stakes. Individual male redwings' movements were plotted on field maps between the hours of 0600 and 1100; 1600 and 1800 EST. By connecting the outermost points, territorial boundaries were delineated according to the method of Odum and Kuenzeler (1955).

During the first half of the pre-breeding season, 20 March to 8 April, males' territories in Segment F were recorded. All birds observed were studied for hourly intervals during all designated time periods throughout the day. This method aided in alleviating any disproportionality in data for individual birds due to time of day, such as frequency of trespassers, activity level, or female chase rate. Trespass rate, the number of males trespassing within a given male's territory per hour, was noted. Trespass rate is an indicator of adult male population pressure to occupy an individual adult male's territory. This may vary with the quality of the territory or the resident adult male's ability to defend his territory. Activity level was recorded as the number of times a male redwing landed on various perches within an hourly interval, and may be indicative of how active an individual bird is in courting females and in defending his territory both intra- and inter-specifically.

Beginning 8 April, males were removed from their territories by means of a Glencoe tree trap placed within a given male's territory. The territorial male would respond aggressively to the decoy, an adult male redwing, situated in one-half of the rectangular trap, but the trap was relatively inefficient. It took several weeks to capture four of the five males in Segment F.

Half the males captured were treated as control birds and half as experimentals. Cotton soaked with alcohol was applied twice to each epaulet of the control male. Cotton soaked with alcohol was applied once to each experimental male's epaulets followed by application of Nyanzol D-black dye (Melchior and Iwen, 1965). Colored leg streamers in varying combinations were then fastened securely around the legs of each experimental and control male. After treatment, each male was placed in a holding cage for 10 minutes so his feathers could dry before he was released near his territory.

During the later half of the pre-breeding period, 15 April to 30 April, males' territories in Segment F were mapped. Female chase rate, the number of times a male chased a female in an hourly interval, was recorded along with male trespass rate and activity level. Female chase rate may be indicative of the number of females within a given male's territory, of the stage of courtship between a resident male and his females, or of the degree of difficulty a given resident male experiences with regard to maintaining his females. Behavioral observations such as dominance relationships between neighboring males, tolerance of subadult males by resident adult males, and female or neighboring adult male responses to a resident male with blackened epaulets were also recorded. Subsequent to a given male's capture and release, it was noted whether or not he returned to his territory and was able to successfully defend it or was displaced by a neighboring or new adult male redwing.

On 1 May Segment C was subdivided into 50-ft. squares in preparation for recording data during the post-breeding period. Mapping and recording data for males in Segment C was performed during the first half of the post-breeding period, 7 May to 14 May, as described above. Between 14 May and 16 May, 8 of the 12 males resident in Segment C were removed from their territories. Easy removal of the males from their territories was made possible by an improved trap designed by Smith (1972). Half of these males were treated as controls and half as experimentals. Mapping territories and recording data for the 8 males captured and released continued during the later part of the post-breeding period, 16 May to 1 June.

OBSERVATIONS AND RESULTS OF THE PRE-BREEDING PERIOD IN SEGMENT F

(20 March to 1 May)

Six males were seen to have established territories. The average territorial size was 54, 859 square feet ± 10.034 (SE). Male trespass rate averaged 2.23 ± 0.48 ($n = 10$). Activity level averaging 18.5 ± 4.5 ($n = 11$) appeared to increase from 21 March to 2 April.

Trapping of Males (April 8 to April 20). One of the six males left his territory. Four of the remaining five males were captured and released. Two of the males were treated as controls and two as experimentals. The remaining male did not respond to the Glencoe tree trap.

Later Half of the Pre-Breeding Period (9 April to 1 May). Average territorial size was 72,505 square feet ± 18,673. One of the experimental birds, #4, captured and released, initially, experienced a higher than average trespass rate. This male, however, was able to maintain his territory without much further interference. The other experimental male, #6, experienced a fairly high trespass rate due to the persistent intrusion on his territory by a new adult male redwing. Both control males demonstrated

little or no increase in trespass rate, and were able to maintain their territories (fig. 1). Experimental males showed a decrease in female chase rate as the prebreeding season progressed while control males showed an increase. Experimental males displayed slightly higher activity levels for this period than did the controls (fig. 1).

POST–BREEDING PERIOD IN SEGMENT F
(1 May to 1 June)

The new adult male redwing continued its intrusion upon the experimental male, #6's, territory. Experimental male, #4, was able to maintain his territory, but experienced a slightly higher than average trespass rate when compared to the control males. Overall, trespass rate tended to decrease from 1 May to 1 June (fig. 1). Experimental males demonstrated higher female chase rates than those of control males (fig. 1) but as the season progressed female chase rate tended to decrease for both groups. Female chase rate decreased earlier for controls than for experimentals. Experimental males were observed to have greater activity levels than control males. Activity level curves for control and experimental males appear to correlate in both groups with trends for both male trespass rate and female chase rate (fig. 1). Nine nests were built in Segment F. Sub-adult males were observed to be somewhat tolerated by resident males around 5 May.

FIRST HALF OF THE POST–BREEDING PERIOD IN SEGMENT C
(1 May to 16 May)

There were approximately four times as many males in Segment C per unit area as in Segment F. Eight males' territories were plotted on graph paper. The average territorial size was 19,303 square feet ± 2,911. The average trespass rate was 0.53 ± 0.30 ($n = 20$) and showed no apparent trend of increase or decrease. Female chase rate tended to decrease. In general, activity level tended to increase from 7 May to 14 May for all eight males.

Trapping of Males (14 May to 16 May). Eight of the 12 males in Segment C were captured with the Smith (1972) trap. Four were treated as controls and four as experimentals.

LATER HALF OF THE POST–BREEDING PERIOD IN SEGMENT C
(16 May to 30 May)

An experimental male, #1, upon release was attacked physically on his territory by the sub-adult male previously tolerated on male #1's territory. Experimental male, #1, subsequent to 14 May, the date of his capture, was no longer seen in the area. On 16 May, a new adult male redwing appeared and was seen to occupy the eastern section of experimental male #1's territory. The territory was then divided between a new adult male redwing and a sub-adult male. The sub-adult male appeared to defend a female's nest site in his territory, but spent more time off his territory than did the resident adult male. Neighboring control male #2 maintained his territory. On 26 May, the new male occupying experimental male #1's territory was no longer seen. Male, #2, then expanded his territory to include this new section, or the eastern half of male #1's territory. The new male's female had appeared to spend much time near bordering male #2's territory previous to new male #1's disappearance.

Of the four experimental males, two had trespass rates of zero ($n = 4$) previous to treatment. The other two had average trespass rates of 1.5 ± 0.59 ($n = 4$) and 0.5 ± 0.34 ($n = 4$). Subsequent to treatment, both males that had trespass rates of zero maintained their territories and their trespass rates increased to 0.08 ± 0.08 ($n = 6$) and 0.33 ± 0.21 ($n = 6$). The two males having average trespass rates of 1.50 and 0.50 were replaced by new adult male redwings. The respective new adult male trespass rates were 0.25 ± 0.25 ($n = 4$) and 0.86 ± 0.70 ($n = 7$).

Of the four males treated as controls, two maintained their territories and one was later forced off his territory by a neighboring new adult male redwing. These three males had average trespass rates of 0.67 ± 0.17 ($n = 3$); zero ($n = 3$); and 0.75 ± 0.48 ($n = 4$) previous to cap-

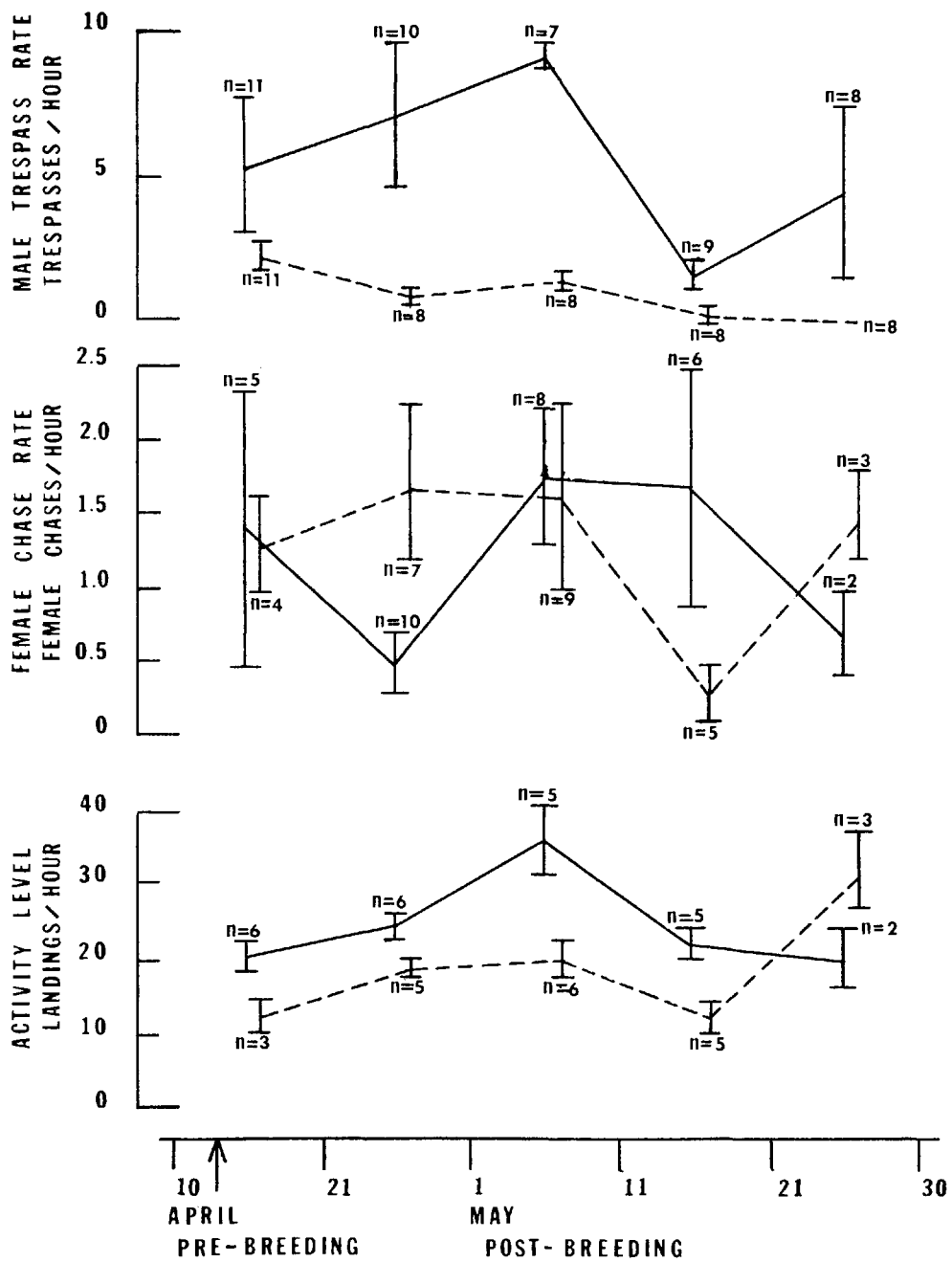

FIGURE 1. Male trespass rate, female chase rate, and activity level are compared for the two experimental males and two control males in Segment F during the pre-breeding and post-breeding periods. Males were treated and released between 9 April and 21 April as indicated by arrow. Values are expressed as the mean ± one standard error of the mean (SEM). Control is dashed line and Experimental is solid line.

ture. The one control male having the highest average trespass rate; 1.0 ± zero (n = 2) when compared to the other three males was displaced by a new adult male after treatment.

Male trespass rate during the latter part of the post-breeding period appeared to show a slight decrease for control males and a slight increase for experimental males maintaining territories. Male trespass rate increased for new males as the season progressed (fig. 2). This was manifested mainly in increased bordering clashes. Experimental males maintaining territories and new males replacing either experimental birds or control birds generally demonstrated a higher female chase rate than did control males. Experimental and control males maintaining territories showed a decrease in female chase rate as the season progressed, but the new males showed an increase. In general, new males demonstrated a higher average activity level when compared to experimentals and controls. The experimentals, in turn, showed slightly higher activity levels than did the controls (fig. 2).

The figures 1 and 2 depict trends in trespass rate, female chase rate, and activity level for experimental and control males in Segment F and Segment C. Statistical comparison of the means, however, cannot be made due to the small sample size.

DISCUSSION

A male redwing's ability to defend his territory from conspecifics was weakened by blackening his red epaulets or shoulder patches during both the pre-breeding and post-breeding periods of this study. Both experimentals experienced higher trespass rates than both controls during the pre-breeding period (fig. 1). The experimentals and controls; however, were able to maintain their territories. Lack of displacement of experimental resident adult males from their territories by either new adult males or neighboring males may have been a result of the abnormally low productivity of marsh Segment F. Smith's (1972) findings supported the assumption that the new adult male redwing population is selective in terms of habitat quality of the territory it will occupy. In Segment F, the average territorial size of 54,859 square feet ± 10.034 (SE) was well above the norm of 3,550 square feet reported by Nero (1956b). The male may have compensated to a change in balance of the marsh ecosystem towards a drier successional stage by increasing the size of its territory to satisfy its nutritional, nesting, and general space requirements. Orians (1964) noted a case in which a male redwing expanded his territory after a particular marsh was burned in order to compensate for a more sparse distribution of cattail growth. In Segment C, studied during the post-breeding period, average territorial size was 19,303 square feet ± 2,911. There were approximately four times as many males per unit area as in Segment F. Another striking comparison between both Segment F and Segment C was the number of nesting females. There were from one to seven females for each resident adult male. Fifty-seven nests were sited in Segment C as compared with five in Segment F. The percentage of nesting females is a more sensitive indicator of general productivity of an area than the number of males. Whether the females are attracted to a more aggressive male defending a better habitat, or just to the habitat itself, or a combination of both is questionable. In Segment F a new adult male redwing occupied the same territory as a resident adult male. This experimental male was observed to chase the new male within his territory throughout the breeding season. In this case, neither male responded hormonally to a great enough degree to take over the territory. This phenomenon has not been recorded in the existing literature and is probably a product of the abnormal situation. Early territorial breakdown in Segment F was also indicative of an area low in productivity. According to Nero (1956b) territorial boundaries are well defined and fixed throughout a breeding season as was found to be the case for territorial boundaries in Segment C. The territorial boundaries in Segment F overlapped to a much greater degree and observation of territorial borders began to breakdown much earlier in the season than in Segment C.

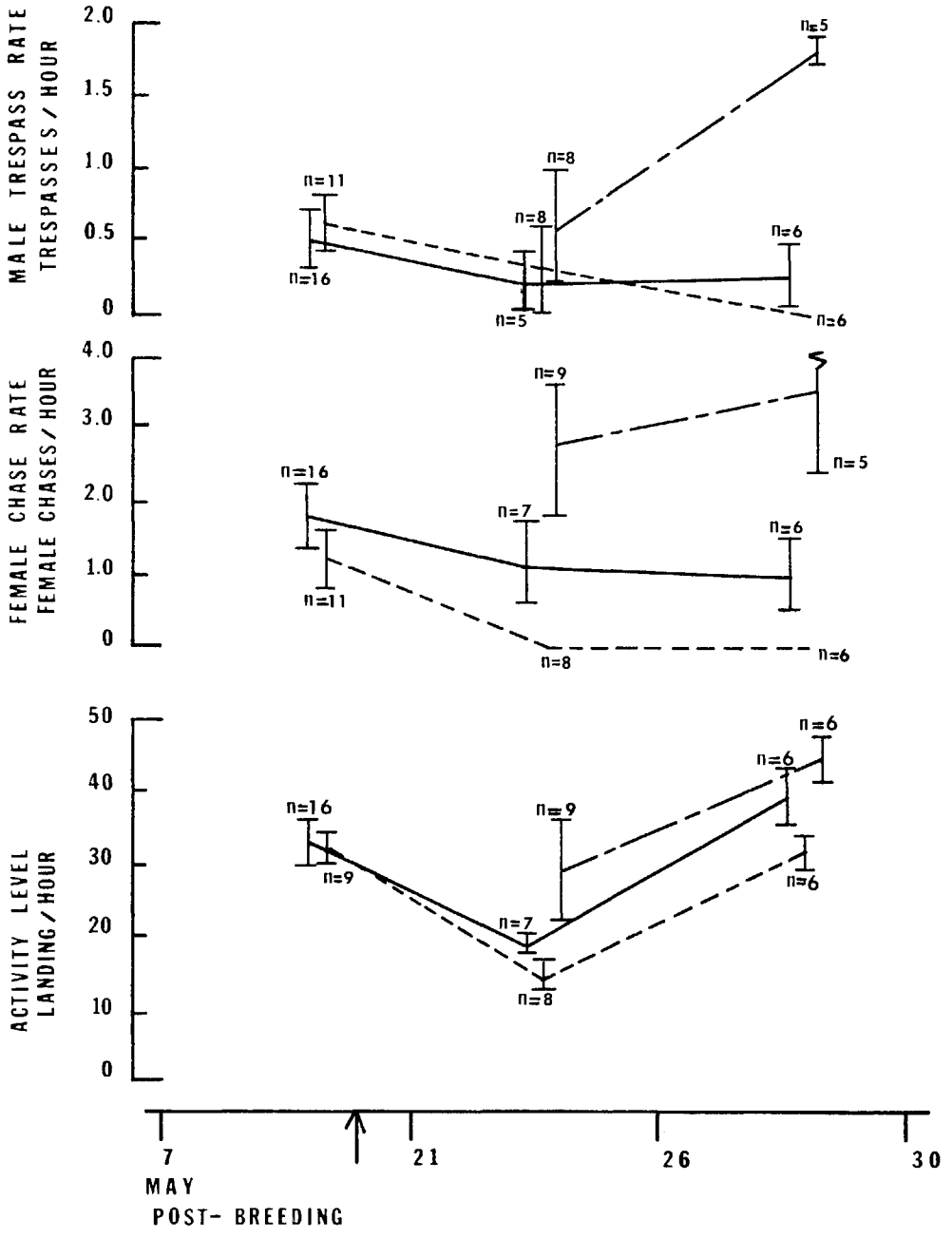

FIGURE 2. Male trespass rate, female chase rate, and activity level are compared for the four control and four experimental males in Segment C during the post-breeding period. Males were treated between 14 May and 16 May as indicated by arrow. Observations for a new male group that displace either control or experimental resident males following their treatment and release is illustrated by the dash dot line. Values are expressed as the mean ± SEM. Control is dashed line and Experimental is solid line.

During the post-breeding period in Segment C new adult male redwings not previously seen to occupy a territory in the area were predisposed to do so. This finding is in accordance with the results of Smith's (1972) study. In Segment C, both experimentals had trespass rates of zero (n=4) prior to treatment and were able to maintain their territories subsequent to treatment. Experimental males having trespass rates of 0.5 ± 0.34 (n=4) and 1.5 ± 0.59 (n=4) prior to treatment, however, were displaced by new adult male redwings subsequent to treatment. Of the four males treated as controls, two maintained their territories and one was later forced off his territory by a neighboring new adult male redwing. These three controls, respectively, had trespass rates of 0.67 ± 0.17 (n=3), 0.75 ± 0.48 (n=4) and zero (n=3) prior to treatment. The single control having the highest trespass rate of $1.0 \pm$ zero (n=2) prior to capture was immediately displaced by a new adult male subsequent to treatment. This indicates that new adult male redwings probably are selective of the territory they will occupy. Both displaced experimental and control birds were prevented by new or neighboring males from resettling on their old territories. Experimental and control males did not appear to differ significantly in their replacement by new adult male redwings.

Determining the significance a particular color pattern plays in behavioral interactions within a species is difficult. A color pattern may function in one type of behavioral interaction and play little or no role in another. Smith (1972) found that males with blackened epaulets were able to mate and maintain their females without much difficulty. He concluded that the red epaulets played virtually no role in mate attraction. But Peek (1971) reported that males blackened prior to mating were unable to attract a mate and concluded that the red epaulets function in mate attraction. As shown from the results of the present study, a male with blackened epaulets may mate and bring off a brood, but he does experience some initial difficulty in attracting and maintaining his mate. Experimental males showed a slight decrease in female chase rate after treatment in comparison to an increase displayed by control males during the pre-breeding period (fig. 1). This may indicate that a greater percentage of the experimental male's energy, at this time, was directed to chasing increased numbers of trespassing males from his territory rather than in normal pre-copulatory behavior. Male-female chase rate in Segment F during the post-breeding period appeared to decrease probably because mating had occurred and other activities such as nest building and incubation had begun. The experimentals, however, displayed a higher average female chase rate than did the controls. Normal behavioral interactions between experimental males and females may have been interrupted due to increased external disturbance in the experimental male's territory. The females in turn, probably were not behaving normally at this point in the breeding sequence due to a previous lack of normal male courtship behavior. In Segment C during the post-breeding period, the female chase rate appeared to decrease as the season progressed. Prior to treatment the group designated as control males did not appear to differ significantly in female chase rate from the group designated as experimental males. After treatment, the controls that maintained their territories showed a lower female chase rate than either the experimental males that maintained their territories or the new adult male redwings. In comparing female chase rates between the new adult male redwings and the experimental group, the new male group showed the higher chase rate (fig. 2). A new adult male occupying territory later in the season may have to physiologically adjust to a new habitat. This male may respond to the new situation by chasing females more. The females, in turn, may not respond immediately to the advances of an unfamiliar male. Because the new males' chase rates were higher on the average than the experimentals maintaining territories, familiarity in terms of behavior patterns probably plays a greater role in normal male-female behavioral interactions than does the normal epauleted pattern. It appeared that a larger percentage of the females re-

mained within their territories after the male had been treated, which may indicate a more positive female response to the nest site than to a particular territorial male.

Familarity among neighboring males probably plays a large role in maintaining a stable territorial system. Experimental male #6 in Segment F was never observed to chase neighboring aggressive experimental male #4. His chasing behavior was fully directed towards the new adult male redwing in his territory, which may demonstrate experimental male #6's recognition of established dominance of the neighboring male #4. The redwing is probably able to distinguish between a new intruder and a resident male (even one whose epaulets have been blackened), due to certain behavior patterns peculiar to a given male. The control male #5's territory in Segment C bordered the new male #7's and experimental male #4's territory. Male #5 was forced off his territory which was subsequently occupied by the new male #7. Male #5's exclusion from the area may have been caused by an upset in the stability of the territorial system in Segment C. The new male, due to a lack of familiarity with bordering control male #5, engaged in more bordering clashes than had the previous resident male.

During the pre-breeding period of the redwing cycle, activity level was higher on the average for the experimentals after treatment than the controls (fig. 1). By increasing his activity, the experimental male exerts a greater amount of energy towards bringing the system back to a stable level so that breeding success is not reduced. Activity level appeared to increase during the first half of the post-breeding period in Segment C, because males now had to defend their territories both inter-specifically as well as intra-specifically. Prior to treatment there is no difference in activity levels between the groups later designated as either control or experimental (fig. 2). After treatment, however, the new adult males showed a higher average activity level than either control or experimental males maintaining territories. The experimentals, in turn, showed higher activity levels when compared with the controls. The new male encounters an increased amount of new external stimuli such as new neighboring males, new females, and new habitat. He responds to this new situation through an increased activity level so that these interactions may be brought to a more stable or familiar level. Toward the end of the post-breeding period, the experimental and control males that maintained their territories showed a pattern of decrease in activity level. This was at a time when most of the young were fledged and there was less need for territorial defense. The new males' activity levels at this time began to increase, probably due to a delay in the activation of their hormonal levels. All males showed an increase in activity level at the end of the post-breeding period probably at a time nearing territorial breakdown.

New adult male redwings were seen to occupy territories in place of former resident experimental or control males during the post-breeding period of this study. These new males may or may not have held a territory and bred earlier in the season. This could not be determined from the study and can only be speculated upon. The new adult male redwings may have abandoned former territories because they were less productive than the territories in the study area. They also may not have held a territory previously due to lack of availability. In this case, territorial behavior may be limiting breeding density for these marsh-nesting birds. There may be several advantages for an individual adult male redwing to occupy a territory late in the season. He may be able to mate in late May or June or he may gain easier access to a productive territory for the following breeding season. Natural selection favors the viability of a species through selection of its most fit individual members in areas of high productivity.

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THE ADAPTIVE SIGNIFICANCE OF SCATTER HOARDING IN THE EASTERN CHIPMUNK.[1] Hoarding of food has evolved in several families of mammals and is especially prominent in the sciurids. Ewer (1968) discussed two distinct types of hoarding, scatter and larder. Scatter hoarding is found in the tree squirrels (*Sciurus*) where small quantities of food are dispersed in shallow pits dug throughout the home range. Larder hoarding is characteristic of semi-fossorial sciurids which cache food within burrow systems (*Eutamias, Tamias, Spermophilus*), and is adaptive by insuring an energy source during winter that is not easily exploited by other species.

While studying the social organization and behavior of a marked population of eastern chipmunks, *Tamias striatus*, scatter hoarding was observed. To my knowledge, this behavior has not been reported in *Tamias*. Scatter hoarding was recorded in four adults on 12 occations during approximately 300 hr of behavioral observations. Individual acorns (*Quercus* spp.) were placed in a shallow depression (2 cm) dug with the forelegs and covered with leaf litter and soil using the nose and forelegs. This behavioral sequence was strikingly similar to that described in the gray squirrel (*Sciurus carolinensis*) by Bakken (1959).

Scatter hoarding commenced with the onset of acorn availability (early September) and was generally observed after periods of eating. Individuals displaying this behavior were not seen to larder hoard until several days later. No chipmunks buried food after 24 September, and all food cached after this date consisted of larder hoarding which continued until winter torpor (late October in adults). The low frequency of occurrence and the appearance of this behavior pattern within a relatively short period of the annual activity cycle of this species may explain why scatter hoarding has not been reported previously.

Why a hibernating species exhibits scatter hoarding behavior is unclear, but two possible hypotheses can be proposed for this behavior. *Tamias* is a shallow hibernator and undergoes periodic torpor from 1 to 6 days from October to March (Panuska, 1959). Chipmunks are often sighted during the winter months (Yerger, 1953), and the burying of food near hibernation sites would insure a ready food source to sustain above-ground activity for winter periods when food availability is minimal. From studies of other sciurids one would expect food to be buried in the vicinity of the burrow system used later as a hibernaculum. Acorns were generally buried within 25 m of the hibernaculum, yet scatter hoarding was not always site specific. In one instance, an adult male buried food 80 m from the hibernaculum. Another male cached food on five occasions near its burrow system but then shifted in early October to a new burrow 76 m from the previous system. Clearly, the energy expended in scatter hoarding must be costly, and would seem to negate the

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hypothesis that scatter hoarding is adaptive for winter survival. Since chipmunks possess relatively small home ranges, distant food caches might be inaccessible during winter hibernation.

The exact origin of *Tamias* is unclear (Black, 1972), yet it is conceivable that the chipmunk and sympatric *Sciurus* evolved together in the deciduous forests of North America. Scatter hoarding may have evolved as a basic component of the behavioral repetoire in the early phyletic history of both species.

The original function of behavior patterns may change if there is a basic change in the way of life of an animal (Mayr, 1970). A behavior may assume a new function or be retained as a behavioral rudiment (Eibl-Eibesfeldt, 1970). As *Tamias* evolved a semi-fossorial way of life with respect to home sites, seeds stored in a burrow may have provided a more reliable and easily defended cache than when stored singly in different places. Scatter hoarding in *Tamias* may thus be a vestigial fixed action pattern; the seasonal transition from scatter to larder hoarding may reflect a sequence of events reminiscent of the phyletic history of food storing behavior in this species.—RICHARD H. YAHNER, *Department of Zoology and Microbiology, Ohio University, Athens, Ohio 45701.*

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